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A COMPARATIVE WOOD ANATOMICAL STUDY OF THE GENUS *DIOSPYROS* L. (EBENACEAE) IN SRI LANKA

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ABSTRACT

A comparative wood anatomical study of 28 *Diospyros* L. species described by earlier workers to be present in Sri Lanka was carried out. The diagnostic features of wood anatomical characters of the taxa concerned were evaluated by employing standard statistical methods such as Principal Component Analysis, Cluster Analysis and Discriminant Analysis. The Sri Lankan fraction of the genus revealed homogeneity with respect to their wood anatomical characters with a dependency range on environmental factors such as water availability. Further based on the wood anatomical characters an attempt was made to establish levels of specialization in order to understand the evolutionary relationships that exist within the species concerned. Even though the evolutionary relationships within the genus are vague, *D. malabarica* and *D. atrata* could be considered as possible ancestral forms from which the Sri Lankan endemic species of the taxon evolved.

Key words: *Diospyros*, comparative wood anatomy.

INTRODUCTION

The history of the "ebony" woods goes back to the Tutankhamun's period, the most famos Egyptian pharaoh ca. 3300 year before (Hora, 1981). Further, it is reported that, Sri Lanka (then Ceylon) was reputed for the best quality "ebony" woods throughout the world from very ancient times (Alston, 1931; Kostermans, 1977). However, proper scientific names of such taxa have been dated from the period of Dutch occupation in parts of Sri Lanka. For instance, Hermann (1717) reported a species, *Highulhaenda* [now known as *D. ferrea* (Willd.) Bakh.à which Burmann (1737) recognized as *Highulhaenda folio myrti*. Further, Linnaeus (1747) cited *Higulhaenda folio myrti* of Burmann in his *Flora Zeylanica* which according to Kostermans (1981) in the present concept is *D. ferrea* (Willd.) Bakh. Thwaites (1864) described 11 new species of *Diospyros* L. from Sri Lanka namely, *D. acuminata* Thw., *D. acuta* Thw. , *D. affinis* Thw., *D. attenuata* Thw., *D. insignis* Thw., *D. moonii* Thw., *D. oblongifolia* Thw. , *D. oocarpa* Thw. , *D. oppositifolia* Thw., *D. quaesita* Thw. He recognized two varieties within *D. embryopteris* [now known as *D. malabarica* (Desr.) Kostel] var *nervosa* and *atrata* which were considered endemic to Sri Lanka and also recognized and described a new species, *Macreightia oblongifolia* Thw. of the genus *Macreightia* of De Candolle (1844), which Kostermans (1981) later named as *Diospyros oblongifolia* (Thw.) Kosterm. Further, Thwaites (1864) recognized three varieties of *Maba buxifolia* var. *ebenus* Thw., var. *microphylla* Thw., and var. *angustifolia* Thw. and he was of the opinion that these three varieties were closely related or connected together by intermediate forms thereby representing a variable species with broad limits. Kostermans (1981) named these varieties as *Diospyros ebenoides* Kosterm., *Diospyros nummulariifolia* Kosterm. and *Diospyros rheophytica* Kosterm. respectively.

Trimen (1893) recognized two genera, *Maba* Forst. and *Diospyros* L., and incorporated the then known taxa of *Macreightia* DC. within the genus *Maba* Forst. Wright (1904) published a comprehensive monograph of the Sri Lankan *Diospyros* L. and his work became a land mark study for the genus in Sri Lanka. He described morphological, anatomical and other taxonomical characters of 20 representative species of *Diospyros* L. in Sri Lanka. However, the genus *Maba* Forst. was excluded from the Ebenaceae. Worthington (1959) recognized 13 species of Sri Lankan *Diospyros* L., based on their morphological characters, of which three species were considered endemic to Sri Lanka, *viz*., *D. crumenata* Thw., *D. quaesita* Thw. and *D. ovalifolia* Wight. However, *D. ovalifolia* Wight is also reported from South India. (Kostermans, 1981; 1977) described two new endemic species, *D. koenigii* Kosterm, a species found only in Gannoruwa forest in Kandy District, and *D. zeylanica* Kosterm from Kanneliya forest near Hiniduma, Galle District. However, Kostermans (1981) in the Revision of the Ceylon Flora excluded this latter taxon stating that this

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plant represents probably a *Stemonoporus* (Dipterocarpaceae). Kostermans (1977) incorpora- -ted other taxa recognized by Thwaites as *Maba* and *Macreightia* within *Diospyros* as described in first paragraph. In addition Kostermans (1981), described yet another variety of *D. insignis*, D. *insignis* var. *parvifolia*. Further he included *Diospyros discolor* Willd. (*D. blancoi* A.DC) [Velvet apple (E)], a species from the Philippines, now occasionally cultivated and naturalized in parts of the island, within the Flora of Sri Lanka totaling the number of species to thirty two. Jayasuriya (1998) added a further endemic species, *D. pemadasai.*

All the revisions of the genus mentioned above have been based mainly on field observations and on morphological characters. Apart from the anatomical observations made by Wright in 1904 with then available facilities, no major anatomical study has been undertaken to determine the species limits to gain a better understanding of the Sri Lankan fraction of the genus.

The present study is an attempt to investigate the wood anatomical characters and ecological parameters, with the idea of understanding the species limits of the Sri Lankan taxa of the genus *Diospyros* L. and comparing such findings with finding of other workers.

MATERIALS AND METHODS

Fresh wood samples of 28 species (Table 1), out of the 32 reported by Kostermans (1981) were collected from the field along with voucher herbarium specimens in triplicate. Collection of specimens was made to include wet, dry and intermediate zones. Further, species which were reported to be strictly confined to certain places were collected (Fig. 1). Four species were excluded since they were reported to be very rare or extinct (Kostermans, 1981). Collected specimens were identified by consulting Trimen (1893), Kostermans (1981) and comparing with the specimens deposited at the National Herbarium, Royal Botanic Gardens, Peradeniya (PDA). Wood samples were taken from straight branches as far as possible, to avoid inclusion of tension or pressure wood. An attempt was made to collect mature wood with maximum diameter whenever possible.

Collected wood samples were cut into pieces of ca. 1 x 1 x 1 cm cubes and preserved in 70% alcohol. Radial, tangential and transverse sections were taken using a Sliding Microtome (E. Leitz Wetzla, Germany) at thickness ranging from 10 - 15 μm., stained in Safranin and Fast Green FCF series following Sass (1958) and mounted in Canada balsam.

Wood pieces of the size of match sticks were macerated using a solution of 30% hydrogen peroxide, distilled water and glacial acetic acid(1:4:5), then washed in running water for at least 24 hours, dehydrated, stained and mounted in Canada balsam following Johansen's method (1940).

Characters of wood for comparative anatomy were selected according to Tippo (1964) and Metcalf and Chalk (1989). Length of the vessel elements was measured including the tails, based on Chalk and Chattaway (1934). Tangential vessel diameters, vessel wall thicknesses and vessel frequencies were measured using cross sections. Individual pores were counted following Wheeler (1986). Measurements of vessel frequencies were based on 25 counts in an area of 2.8 mm^2 field of view.

Ray types were described according to Kribs (1935). The terminology used for microscopic features was based on the International Association of Wood Anatomists' list of microscopic features for hardwood identification (IAWA Committee, 1989). Tangential wood sections were used to measure ray heights and ray frequencies while the lengths of fibers were measured using macerated tissues. Relative cell sizes and vessel frequency are given in accordance with Chattaway (1932).

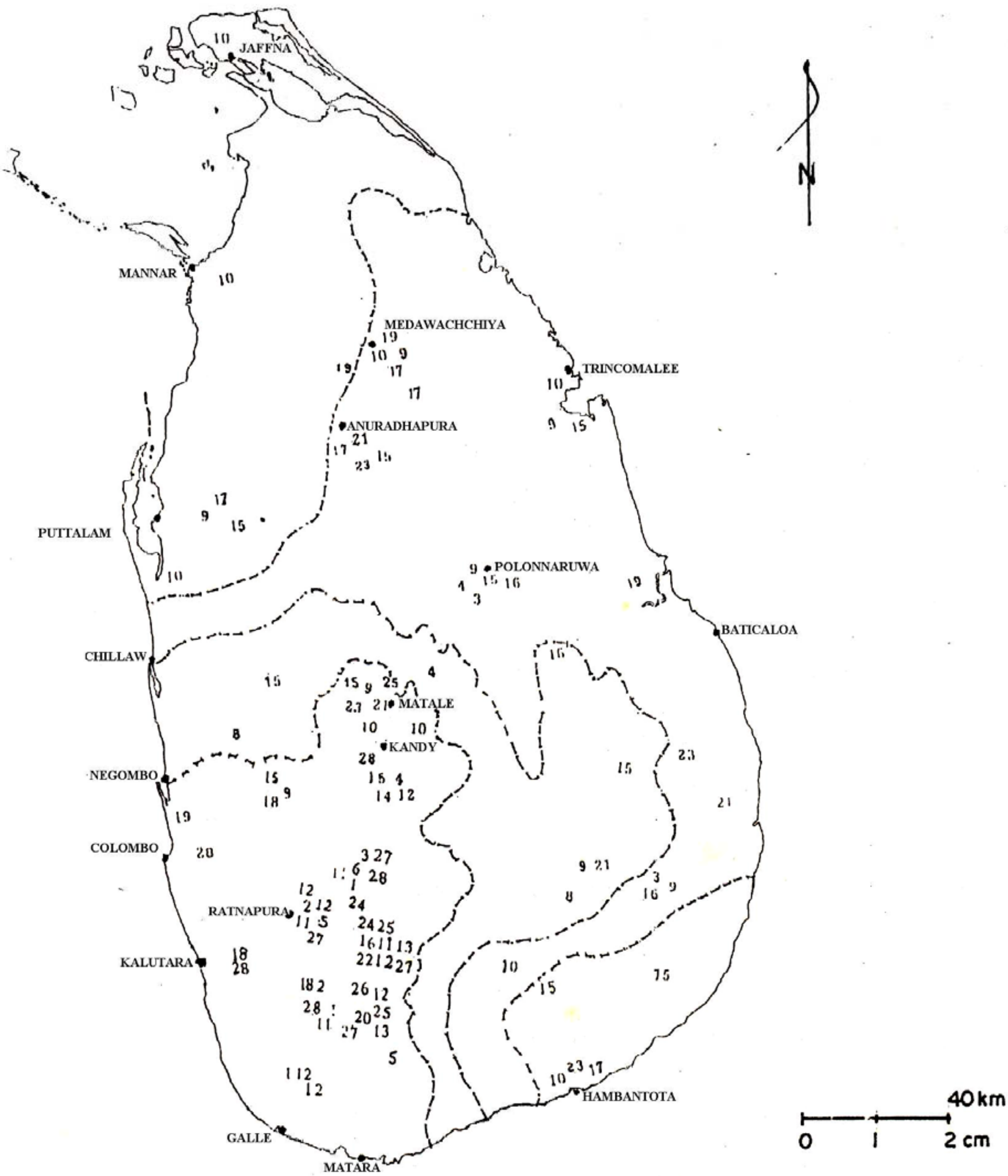
For quantitative data macerated wood, cross sections, radial sections and tangential sections were measured under the low power (x 10) and high power (x 40) of an Olympus PM – 10 DAD light microscope.

Annual rainfall and mean annual temperatures were obtained from the Meteorological Department, Colombo. Altitudes of the areas where specimens were collected were determined using the altimeter supplemented with topographic sheets of the Survey Department (1992). Agro-ecological zones (Fig. 1) identified were based on the soil map of Sri Lanka (Irrigation Department, 1988).

Statistical Analysis

The basic statistical analysis was done according to procedures outlined by Snedecor and Cochran (1967) and Sokal and Rohlf (1981). For each sample from each species a mean value with 95% confidence interval of wood anatomical features was calculated. These values were tabulated with the species description citing mean ranges of

Figure 1.



Distribution of *Diospyros* in Sri Lanka [modified after Kostermans (1981)]. *D. acuminata* (2) *D. acuta* (3) *D. affinis* (4) *D. atrata* (5) *D. attenuata* (6) *D. chaetocarpa* (7) *D. discolor* (8) *D. ebenoides* (9) *D. ebenum* (10) *D. ferrea* (11) *D. hirsuta* (12) *D. insignis* (13) *D. insignis var. parvifolia* (14) *D. koenigii* (15) *D. malabarica* (16) *D. melanoxylon* (17) *D. montana* (18) *D. moonii* (19) *D. nummulariifolia* (20) *D. oblongifolia* (21) *D. oocarpa* (22) *D.oppositifolia* (23) *D.ovalifolia* (24) *D. quaesita* (25) *D. racemosa* (26) *D. rheophytica* (27) *D. thwaitesii* (28) *D. walkeri.*

species and maximum and minimum intervals within parenthesis. For statistical analysis, mean values of each species were tabulated. Mean values derived were then used for fundamental statistical analysis such as mean comparison and analysis of variance. Further, Pearson product movement correlation was sought for the quantitative data to find out any interdependencies of anatomical characters. The same statistical techniques were employed to trace the relationships between ecological parameters such as altitude, mean annual rainfall and mean annual temperature. The correlation obtained was used to calculate r^2 (coefficient of determination) to find dependency of the anatomical features over ecological parameters. The extent of influence of ecological parameters on wood anatomical features was sought in order to ascertain the degree of dependency between the two. The collected specimens were assigned to the climatic zones following Mueller-Dombois (1968) and further assigned to agro-ecological groups based on the soil map of Sri Lanka (Irrigation Department, 1988). Subsequently, mean vessel element lengths and mean fiber lengths were plotted separately with agro-ecological zones to detect whether there are any ecological patterns reflected. The codes used in investigating quantitative and qualitative characters and numerical codes used in qualitative analysis are given in Tables 2.A and 2.B.

Multivariate analytical techniques, adopted by Sneath and Sokal (1973), Gauch (1986), Burley and Miller (1989) were attempted for further analysis. Principal Component Analysis (PCA) and Cluster Analysis (CA) were attempted in order to examine the taxonomic patterns of the data and to generate a classification system. In the course of statistical analysis, the species were coded with a number and an acronym as shown in Table 1.

The original data were converted into standardized scores i.e. Z-scores (with 0 mean and standard deviation of 1) in order to give an equal weight to all the measurements. Phenetic similarity or dissimilarity was also calculated.

The mesomorphy index (Carlquist and De Buhr, 1977) was calculated for the specimens since this index is reported to be related to the habitat preference. Another index, conductivity suggested by Carlquist (1984), was also calculated for each specimen because this index is believed to be a measure of vulnerability of vessels to extreme tensile forces created by extreme drought and cold conditions. Mesomorphy index and conductivity values were calculated by using the following equations:

$$\text{Mesomorphy} = \frac{\text{Vessel length x Vessel diameter}}{\text{Vessels per mm}^2}$$

$$\text{Conductance} = \frac{(\text{Vessel diameter})^4 \text{ x } 0.0001}{\text{Vessels per mm}^2}$$

All the computations and statistical analyses were done using the statistical program package SPSS/PC+ Statistics ™ 4.0 and Windows version 6, (SPSS Inc., 1993).

RESULTS AND DISCUSSION

The occurrence of growth rings was not consistent among the species of Sri Lankan fraction of *Diospyros* L. Certain species showed very faint and discontinuous growth rings marked only by rather thick-walled fibers (Table 3). However, a number of non-endemic dry zone, intermediate and low country wet zone species lack in growth rings meanwhile some non-endemic dry, intermediate species and endemics of low country wet zone species showed discontinuous growth rings indicating that there was no considerable relationship between endemicity or with the ecological origin of the species with growth ring formation. The occurrence of growth rings in tropical woods is, generally, believed to depend on the environmental factors such as photoperiod, temperature and availability of water (Vliet, 1979; Kramer, 1964; Fahn *et al.*, 1985). Therefore, it is evident that fluctuations in temperature, rainfall and altitudinal changes seem to be of little influence on the presence or absence of growth rings within the Sri Lankan species of the genus *Diospyros* L.

Sri Lankan climate lacks the seasonality. However, wet and dry spells are well-recognized all over the island which is directly related to the mean annual rainfall. Therefore, occurrence of growth rings may be attributed to the soil moisture availability which in turn influences the variation in the plant growth.Further, whether the formation of growth rings is associated with the photoperiodism or is influenced by auxins as pointed out by Kramer (1964) is yet to be ascertained and require in-depth investigations.

All the wood examined was non-storied. Individual vessel pores were oval to circular in cross sectional view. The pores were solitary or distributed in radially arranged multiples of varying number of pores (Fig. 2a, d, g).

Table 1. Species of *Diospyros* L. collected for the study and identified according to Kostermans (1981). endemicity, zonal distribution and acronyms used in the study.

Species	Endemicity	Zonal Distribution	Acronym	Code
D. acuminata (Thw.) Kosterm.	E	W	DACUM	1
D. acuta Thw.	E	W	DACUT	2
D. affinis Thw.	NE	D,I	DAFFI	3
D. atrata Alston.	E	W	DATTR	4
D. attenuata Thw.	E	W	DATTN	5
D. chaetocarpa Kosterm.	E	W	DCHAE	6
D. discolor Willd.	NE	W,I	DDISE	7
D. ebenoides Kosterm.	E	I	DEBNO	8
D. ebenum Koenig.	NE	D,I	DEBNU	9
D. ferrea (Willd.) Bakh.	NE	D,I	DFERR	10
D. hirsuta L.	E	W	DHIRS	11
D. insignis Thw.	NE	W	DINSI	12
D. insignis var. *parvifolia* Kosterm.	E	W	DINVP	13
D. koenigii Kosterm.	E	W	DKOEN	14
D. malabarica (Desr.) Kostel	NE	D,I	DMALA	15
D. melanoxylon Roxb.	NE	D	DMELA	16
D. montana Roxb.	NE	D	DMONT	17
D. moonii Thw.	E	W	DMOON	18
D. nummulariifolia Kosterm.	E	D	DNUMM	19
D. oblongifolia (Thw.) Kosterm.	E	W	DOBLO	20
D. oocarpa Thw.	NE	D,I	DOOCA	21
D. oppositifolia Thw.	E	W	DOPPO	22
D. ovalifolia Wight	NE	D,I	DOVAL	23
D. quaesita Thw.	E	W	DQUES	24
D. racemosa Roxb.	NE	W	DRACE	25
D. rheophytica Kosterm.	E	W	DRHEO	26
D. thwaitesii Beddome	E	W	DTHWA	27
D. walkeri Wight	E	W	DWALK	28

E =Endemic, NE = Non-endemic, D = Dry zone, W = Wet zone, I = Intermediate zone

Within the dry zone species such as *D. montana* Roxb., *D. oocarpa* Thw., *D. affinis* Thw. and *D. ovalifolia* Wight, the pores were arranged in multiples of 3-11 in a single group (Fig. 2g). In general, the dry zone species possess higher number of vessel groups per unit area than the intermediate and the wet zone species. Such observations agree with Carlquist (1984) was states that the increased number of groups of vessels indicates a xeric tendency of the habitat of a species.

Metcalf and Chalk (1989) stated that, the number of vessels per square millimeter could be very significant as a taxonomic character only if very low or very high numbers of vessels are encountered. The present study reveals that the non-endemic dry zone species posses higher number of vessels per square millimeter than the endemic wet zone species.

Table 2. A. Codes used in the study for wood anatomical characters.

Character Code	Description
Quantitative characters	
TVEL	Vessel element length in µm
VDIA	Vessel Diameter in µm
VWTH	Vessel Wall Thickness in µm
DFPO	Distribution frequency of pores/mm^2
NGPA	Number of Groups of Pores per area/mm^2
NSPA	Number of Solitary Pores per area/mm^2
GSRT	Groups to Solitary Pores ratio
FLEN	Fiber length in µm
FDIA	Fiber Diameter in µm
RPMM	Rays per millimeter
RHMM	Ray Height in millimeter
RHCE	Ray Height in number of cells
RWMM	Ray Width in millimeter
RWCE	Ray Width in number of cells
Qualitative characters	
VEDI	Vessel Distribution
PERP	Perforation plates of vessel elements
PITS	Pits whether minute or vestured
TYLO	Tyloses present or absent
GRRI	Absence or presence of Growth Rings
FIBR	Fibers thick or thin
RAUB	Rays, uniseriate or biseriate
TVRP	Type of vessel-ray pits
PADS	Axial parenchyma distribution
CRYS	Crystals, Present or Absent

However, such a relationship cannot be generalized for all the dry and wet zone species examined since some of the species, for instance *D. rheophytica*, a species which grows along the banks of rivers and rivulets in the low country wet zone, showed a higher value that does not fit into place along with the idea expressed above. Considering the percentage values of vessel elements per area, Wright (1904) attempted to correlate the higher percentages of vessel elements with thin-leaved trees and lower percentages with thick-leaved Sri Lankan species of *Diospyros*. From an ecological point of view, Wright (1904) was of the opinion that vessel distribution frequencies of the dry zone and the wet zone species could be related to the habitat. The results of the present study agree with Wright (1904) on the basis that the dry zone species show high frequencies of vessel distribution per area, compared with the wet zone.

Working with the Sri Lankan *Diospyros*, Wright (1904) stated that there was no difference in the vessel dimensions between species growing in Mannar where more arid conditions occur, compared with those growing in Adams Peak Wilderness where the climatic conditions are quite different, especially in relation to the moisture availability. The tangential vessel diameters of the wood samples studied ranged from 48.4 to 107.2 µm. On this basis, the observations of the present study agree with Wright (1904). However, Metcalf and Chalk (1989) stated that vessel diameter can vary with samples which are taken from different places of the same tree. Further, Aloni and Zimmermann (1983) have pointed out that the size and frequency of vessels vary along the plant axis in response to concentration gradient of auxins. Kramer (1964) showed that wood formation depends to a great extent on the water availability of the habitat. As such vessel element diameters are of limited value in the delimitation of the taxa under consideration. However, these could be used to draw the generic limits of the Sri Lankan *Diospyros*.

Bailey (1957) and more recently Baas (1976; 1982) believed that the length of vessel elements and other morphological characters such as perforation plates and types of pits reflect the level of specialization of a taxon and further recognized the evolutionary trends of vessel element lengths within angiosperm taxa which came to be known as Bailian trends. Metcalf and Chalk (1989) also stated that the vessel element length is more significant as a measure of phylogenetic specialization rather than as a diagnostic character for a taxon. It is the general opinion of Bailey (1957), Baas (1976; 1982) and Metcalf and Chalk (1989) that the less specialized plant taxa have longer vessel elements than the specialized forms. On this basis, it is interesting to note that the non-endemic species of Sri Lanka have a shorter vessel element length than the endemic species found at wet and higher altitudes, while the taxa of the intermediate zone exhibit vessel element lengths of medium range. On this basis, the endemic *Diospyros* species of Sri Lanka are less specialized than the non-endemic taxa found in the dry zone. Whether these observations indicate a retrogressive evolutionary trend with respect to the Sri Lankan endemic taxa is interesting, however, and needs further investigation before conclusive decisions are made.

Table 2. B. Code words and numerical codes used in qualitative analysis.

Character (Abbreviations in parentheses)	Character State	Code
Vessel Distribution (VEDI)	Exclusively solitary	11
	Radial groups of 3-4	12
	Radial or oblique	13
	Tangential arrangement	14
	Pore clusters	15
Perforation plate (PERP)	Oblique	11
	Transverse	12
Pits (PITS)	Minute	11
	Vestured	12
Tyloses (TYLO)	Present	11
	Absent	12
Growth Rings (GRRI)	Present	11
	Absent	12
Fibers (FIBR)	Thick-walled	11
	Thin-walled	12
Trachieds (TRAC)	Present	11
	Absent	12
Rays (RAUB)	Homogenous	11
	Heterogenous	12
Type of Vessel-Ray Pits(TVRP)	Vertically oriented	11
	Horizontally oriented	12
	Similar to Intervessel pits	13
Parenchyma distribution (PADS)	Diffuse	11
	Paratracheal	13
	Apotracheal	12
	Vertical	14
Crystals (CRYS)	Present	11
	Absent or very rare	12

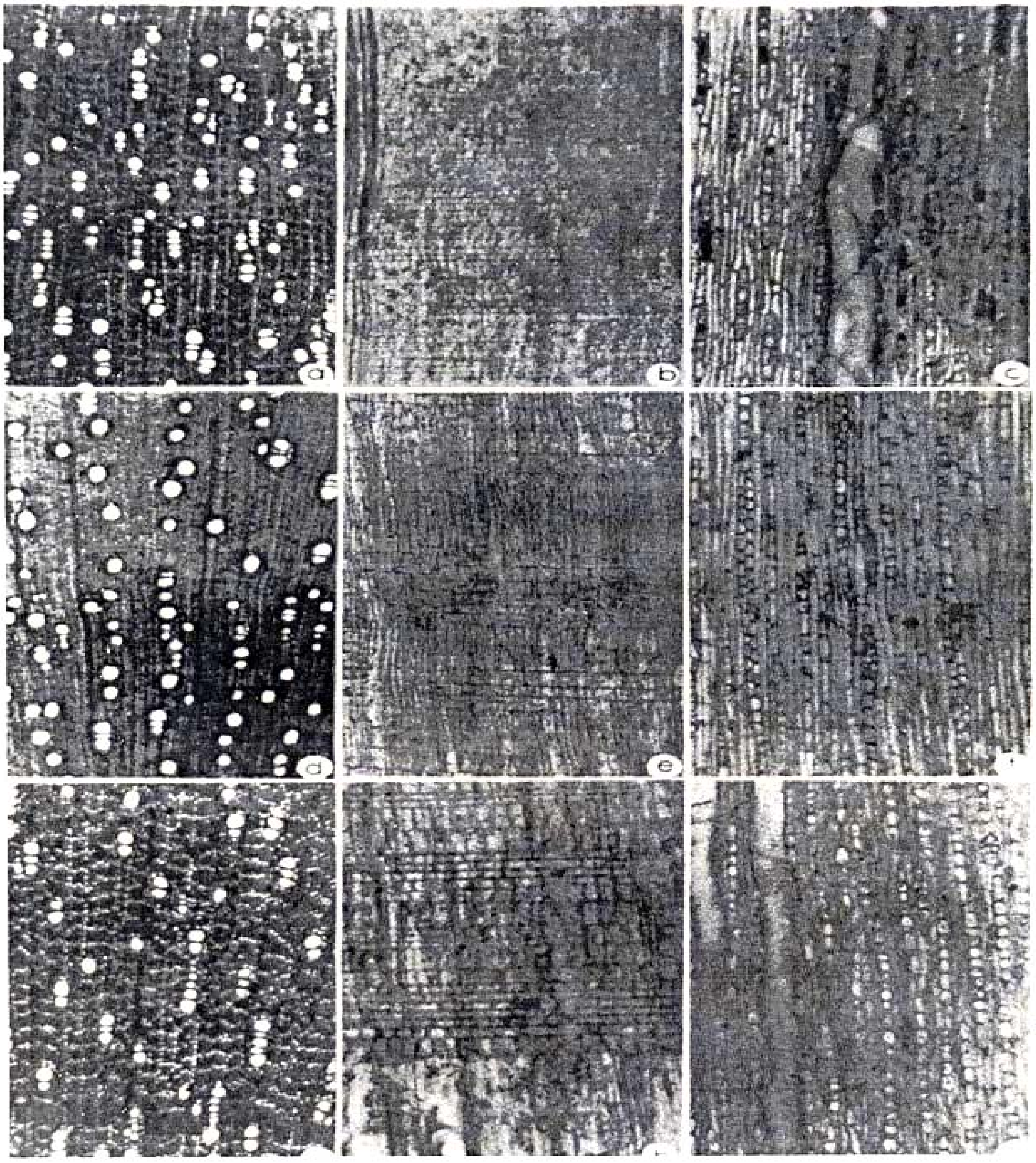


Figure 2. Wood anatomical features of the genus *Diospyros* (a) Cross sectional view of *D. ebenum* x 105. (b) Radial longitudinal section of *D. ebenum* x 660, (c) Tangential longitudinal section of *D. ebenum* x 660, (d) Cross sectional view of *D. moonii* x 105, (e) Radial longitudinal section of *D. moonii* x 660, (f) Tangential longitudinal section of *D. moonii* x 660, (g) Cross sectional view of *D. montana* x 105, (h) Radial longitudinal section of *D. montana* x 660 and (i) Tangential longitudinal section of *D. montana* x 660.

The thickness of vessel element wall ranged from 4.32 - 8.65 μm. The vessel wall thickness of the dry zone species is greater than that of Wet zone areas. Whether such characters observed in the dry zone taxa in relation to the water availability is an adaptive measure of conservation of water resources, needs further studies. Further, it is interesting to note that *D. rheophytica* Kosterm, a species restricted to the wet zone river banks, has the highest vessel wall thickness among the Sri Lankan species. Thus it is possible that further investigations on these lines may show a relationship between the vessel wall thickness and the availability of water.

The terminology of wood fibers is controversial and yet to be resolved (Carlquist, 1986a; 1986b; Baas 1986). However, Metcalf and

Chalk (1989) stated that non-septate fibers do not possess many features of taxonomic interest while septate fibers are often characteristic of large families and are useful as a taxonomic character. The wood fibers observed in the study are non-septate and ranged from 376.00 (302.64 - 444.36) to 2055.00 (1564.66 - 2545.39) μm in length. The distribution of fiber length shows that the fiber length alone as a taxonomic character cannot be related to the level of specialization within the genus studied. An index derived from the ratio between fiber length and vessel element length approaches to one in less specialized woods while higher values indicate higher levels of specialization in secondary xylem in angiosperms (Baretta-Kuipers, 1976). Results indicated a general tendency in which the non-endemic dry zone species of the genus are more specialized than thoseof endemic wet zone species (Table 3).

Table 3. Occurrence of growth rings and the ray histology and ratio between fiber length and vessel element length in Sri Lankan species of *Diospyros* L.

Code	Species	Character		
		Growth Rings	Ray Histology	FVRAT
1	*Diospyros acuminata* (Thw.) Kosterm.	absent	uniseriate	1.6
2	*Diospyros acuta* Thw.	absent	uniseriate	2.1
3	*Diospyros affinis* Thw.	present	uniseriate	2.3
4	*Diospyros atrata* Alston	absent	uniseriate	2.5
5	*Diospyros attenuata* Thw.	present	uniseriate	2.0
6	*Diospyros chaetocarpa* Kosterm.	absent	uniseriate	2.0
7	*Diospyros discolor* Willd.	absent	uniseriate	1.9
8	*Diospyros ebenoides* Kosterm.	present	uniseriate	2.6
9	*Diospyros ebenum* Koenig.	present	uniseriate	2.4
10	*Diospyros ferrea* (Willd.) Bakh.	present	multiseriate	2.5
11	*Diospyros hirsuta* L.	absent	uniseriate	1.9
12	*Diospyros insignis* Thw.	absent	multiser iate	2.1
13	*Diospyros insignis* var.*parvifolia* Kosterm.	present	multiser iate	2.0
14	*Diospyros koenigii* Kosterm.	present	uniseriate	2.2
15	*Diospyros malabarica* (Desr.) Kostel.	absent	uniseriate	2.8
16	*Diospyros melanoxylon* Roxb.	present	uniseriate	2.3
17	*Diospyros montana* Roxb.	present	uniseriate	3.2
18	*Diospyros moonii* Thw.	absent	multiseriate	1.8
19	*Diospyros nummularifolia* Kosterm.	present	uniseriate	2.1
20	*Diospyros oblongifolia* (Thw.) Kosterm.	present	uniseriate	2.2
21	*Diospyros oocarpa* Thw.	present	uniseriate	2.6
22	*Diospyros oppositifolia* Thw.	present	uniseriate	1.8
23	*Diospyros ovalifolia* Wight	present	uniseriate	2.1
24	*Diospyros quaesita* Thw.	present	uniseriate	2.1
25	*Diospyros racemosa* Roxb.	absent	uniseriate	2.4
26	*Diospyros rheophytica* Kosterm.	absent	uniseriate	1.7
27	*Diospyros thwaitesii* Beddome.	present	uniseriate	1.4
28	*Diospyros walkeri* (Wight) Guerke	absent	uniseriate	1.7

The characteristic features of wood ray tissues are of importance in depicting an evolutionary sequence of specialization within angiosperms (Kribs, 1935). Barghoorn (1940) investigated the ontogenetic development and phylogenetic specialization of rays within the angiosperms and agreed with Kribs (1935) and stated that, heterogeneous Type I of Kribs' which consists of a number of layers of procumbent cells with four upright or square marginal cells occurred in the extinct taxa of Benetitales, Pteridospermae, Cycadales and the primitive dicotyledonous species. On the other hand Kribs' Heterogeneous Type III which exhibits procumbent cells with a single row of upright or square marginal cells is considered as a specialized form of rays. However, Barghoorn (1941) cautioned that when considering variations of ray structure for taxonomic purposes, ontogenic variations which might occur during development stages, should also be taken into account. Summarizing all the facts already mentioned on rays, Metcalf and Chalk (1989) further added that uniseriate rays are diagnostically important because of their restricted occurrence and that this feature is particularly characteristic of certain taxa that are phylogenetically advanced but it tends to be typical of individual genera rather than particular species. The present study reveals that, almost all the Sri Lankan *Diospyros* species possess the exclusively uniseriate rays (Table 3) and a few of them possess rays with multiseriate portions as wide as the uniseriate portions (Fig. 2 c, f) and this may be used to split the genus in to two broad groups. However, Wright (1904) recognized three groups on the same basis, (a). medullary rays are one cell in tangential breadth, (b) medullary rays are more than one cell in tangential breadth, and (c) presence of special radial groups of parenchyma.

The present study partly agrees with that of Wright (1904) on the basis that the Sri Lankan taxa belong to exhibit the first two categories. However, the third category with special radial groups *sensu* Wright (1904) was not clearly distinguishable from the findings of the present study. Based on these lines, it is observed that the Sri Lankan species of *Diospyros* under consideration have xylem rays of the Kribs' Heterogeneous Type I and or Heterogeneous Type II. Kribs Heterogeneous Type III which is considered to be the most advanced type (Barghoorn 1940; 1941a), was not observed in any Sri Lankan species studied. Further, Kribs' Homogenous types of rays which are considered more evolutionarily advanced than the Heterogeneous types were also not observed. On this basis, the Sri Lankan taxa cannot be considered as a highly advanced group. With respect to the Sri Lankan species of *Diospyros* the taxa posses Kribs' Heterogeneous Type I rays as observed in the two endemic species *D. atrata* Alston and *D. quaesita* Thw., are less specialized than the taxa that posses Kribs' Heterogeneous Type II rays observed in the non-endemic species *D. affinis* Thw., *D. ebenum* Koenig., *D. oocarpa* Thw., and the endemics *D. attenuata* Thw., *D. ebenoides* Kosterm., *D. hirsuta* L., *D. koenigii* Kosterm., *D. moonii* Thw., *D. oblongifolia* (Thw.) Kosterm., *D. thwaitesii* Beddome.

However, six non-endemic taxa namely, *D. discolor* Willd., *D. malabarica* (Desr.) Kostel., *D. montana* Roxb., *D. ovalifolia* Wight, *D. racemosa* Roxb., *D. melanoxylon* Roxb. and the six endemic taxa namely, *D. acuminata* (Thw.) Kosterm., *D. acuta* Thw., *D. insignis* var. *parvifolia* Kosterm., *D. oppositifolia* Thw., *D. rheophytica* Kosterm. and *D. walkeri* (Wight) Guerke possess both Kribs' ray Types I and II. With respect to evolutionary advancement, the above mentioned taxa could be considered as intermediates. There seem to be no significant evolutionary trends within the Sri Lankan taxa of the genus with respect to Heterogeneous ray Types of Kribs. The non-endemic taxa with Kribs' ray Type II are restricted to the dry zone while the endemics of the same types are found in the wet zone. Further, the endemic taxa with a mixture of Heterogeneous Type of Kribs I and II are distributed in the wet zone while the non-endemics mainly occur in the dry zone. On this basis, the Heterogeneous ray Types seem to have some relationship with environmental factors which needs further investigation.

Kribs in 1937 regarded the absence of axial parenchyma as a primitive character (Metcalf and Chalk, 1989). Metcalf and Chalk (1989), summarizing the work on axial parenchyma distribution by Kribs further stated that the number of cells in a single strand of parenchyma could be considered as an index of level of specialization. Based on the classification of axial parenchyma by IAWA (1989), Sri Lankan *Diospyros* species showed banded parenchyma of reticulate, scalariform or marginal types only. Carlquist (1975) considered the presence or absence of axial parenchyma as an ecological variation rather than any evolutionarily significant feature. On this basis the presence of axial parenchyma within the Sri Lankan taxa is of limited value in the delimitation of the taxa concerned.

The vessel elements of all the species studied possessed simple perforation plates, end-walls transverse or slightly oblique, with short tails.

Hence, it is clear that there is no value of such characters in delimitation of the species. Intervessel pits of all the species observed were minute, alternate, vestured, circular or oval in shape (Fig. 3 a). Vessel-ray pits were also similar to intervessel pits in size and shape throughout the ray cells (Fig. 3 c), in all the specimens examined except *D. ferrea* (Willd.) Bakh., which possess large vessel-ray pits with much reduced borders and horizontally or vertically oriented as well as with normal pits (Fig. 3 d). On this basis, *D. ferrea* (Willd.) Bakh. stands out from the other species of *Diospyros*. Based on morphological characters Kostermans (1981) maintained *D. ferrea* (Willd.) Bakh. as a distinct species where as White (1993) believed that, based on wood anatomical characters this taxon should be placed under a separate section of the genus *Diospyros*. According to the differences found with respect to vessel-ray pits, it could be suggested that *D. ferrea* (Willd.) Bakh. be separated into a Section of the genus as suggested by White (1993).

The formation of tyloses has been considered as an indication of evolutionary primitiveness of angiosperms (Bonsen and Kucera, 1990). Tyloses were observed most of the species studied except *D. chaetocarpa*, *D. acuta*, *D. affinis*, *D. attenuata*, *D. discolor*, *D. hirsuta*, *D. insignis*, *D. moonii* and *D. oppositifolia*. In general, the dry zone species of *Diospyros* possess more tyloses than the wet zone species.

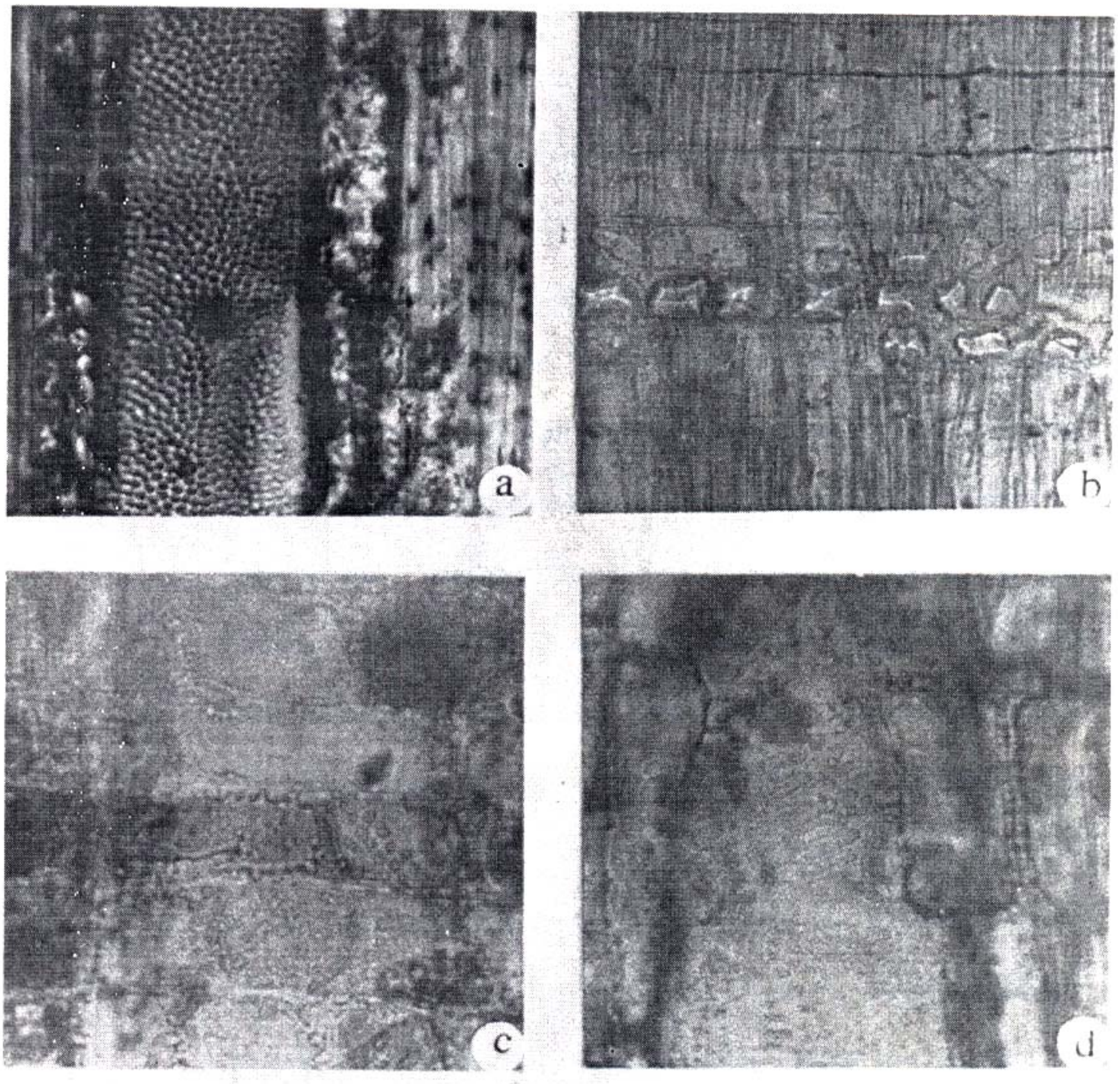


Figure 3. Wood anatomical characteristics of the genus *Diospyros*, (a) Intervessel pits of *D. insignis* x 1320, (b) Crystals in rays of *D. ebenum*. x 1320, (c) Vessel -ray pits of *D. ebenum* x 1320 and (d) Vessel- ray pits of *D. ferrea* x 1320.

Chattaway (1955; 1956) and IAWA (1989), have pointed out that, the absence or presence and if present, the type and location of crystals are of taxonomic importance. Prismatic or rhombohedral crystals were observed in ray cells (Fig. 3 b) in all the species of Sri Lankan *Diospyros* taxa studied. The abundance of crystals varied within the species as well as within specimens from the same species. However, in *D. attenuata* Thw., *D. insignis* var. *parvifolia* Kosterm., *D. malabarica* (Desr.) Kostel., *D. rheophytica* Kosterm. and *D. walkeri* (Wight) Guerke crystals were found very rarely. Crystals were mostly chambered. The occurrence of tyloses and crystals is of limited value in delimitation of the Sri Lankan species of the genus concerned.

Multivariate statistical analyses were applied in the present study to trace the possible relationships between anatomical and ecological features. Sneath and Sokal (1973) and Sokal and Rohlf (1981) have shown the importance of multivariate statistical techniques in numerical Taxonomy. Using multivariate techniques, Jacobseni (1979), Robertse *et al.* (1980) Khidir and Wright (1982) and Hedren (1990) successfully solved the problems in variation between *Allium cernuum* and *Allium stellatum*, wood anatomy of South African *Acacia*, systematics of Graminae and the African complex of *Justicia striata* respectively. The same approach has been made by Somaratne and Heart (2001) and Pathirana and Heart (2004) in establishing the relationships between species of the genus *Calophyllum* and the genus *Garcinia* and to elucidate the possible relationships among the species of *Diospyros* in the present study.

The dendrogram derived from Cluster Analysis (CA) based on quantitative wood anatomical features of the *Diospyros* L. species showed no considerable grouping tendency within the genus (Fig. 4). This finding indicates that taking wood anatomical features one at a time and taking as whole characters simultaneously led to different conclusions. However, based on the results of cluster analysis, it could be stated that wood anatomical features seem to be of limited value in delimitation of taxa within the genus *Diospyros* L. if they are treated individually. Further analysis with other vegetative anatomical data from leaf, young stem and node might be of importance.

In the Principle Component Analysis (PCA), the characters such as pore distribution frequency (DFPO), number of vessel groups per area (NGPA), vessel element length (TVEL) and fiber diameter (FDIA) are heavily loaded along the PCA Axis one and ray height in number of cells (RHCE) and in millimeters (RHMM), and ratio of vessel group to solitary (GSRT), highly influenced the axis two (Table 4). The total percentage variation obtained by the analysis is 71.4 % for the data recorded. The percentage variability explained by axis one and two is 42.3 %. The rest of the components are less significant and could be neglected. Further Table 4 indicates that these wood anatomical characters which are heavily loaded along the components could be considered as important features in separation of species within the genus. The scatter plots derived from the PCA with the idea of tracing the grouping tendency within the genus are shown in the Fig. 5 and 6.

The scatter plots PC 1 Vs PC 2 (Fig. 5) indicate a weak tendency of grouping of specimens. Species such as *D. insignis* and *D. walkeri* were separated as two species. The analysis showed that the above mentioned species are to a certain extent, related wood anatomically and further, closely related to *D. quaesita* Thw. This agrees with Kostermans' (1981) who observed similarity between these two species based on the colour of the wood and Trimen's (1893) observation based on fruit characteristics. The occurrence of plumbagin, Scopaletin and a tri-oxygenated Coumarin in these two taxa, further confirmed their close relationship (Jayasinghe P., 1992, Unpublished data).

The specimens of *D. oppositifolia* fall into an isolated position in scatter plots (No. 22 in Fig. 5 Fig. 6). This is the only species which possesses opposite leaves within the genus except *D. melanoxylon* which possesses sub-opposite leaves. In geographical distribution, it is highly restricted only to the top of southwest face of Haycock mountain in Galle district, at the altitude of 700 m. Wood anatomically, it is difficult to establish any living relationships between *D. oppositifolia* and the rest of the species within the genus.

A group of species which consists of *D. oocarpa*, *D. montana* and *D. ebenum* (21, 17, 9 in Fig. 6) could be considered as closely related species, share the same habitats and are of arborescent habit. This could be attributed to the adaptability of the wood anatomical features to a particular habitat.

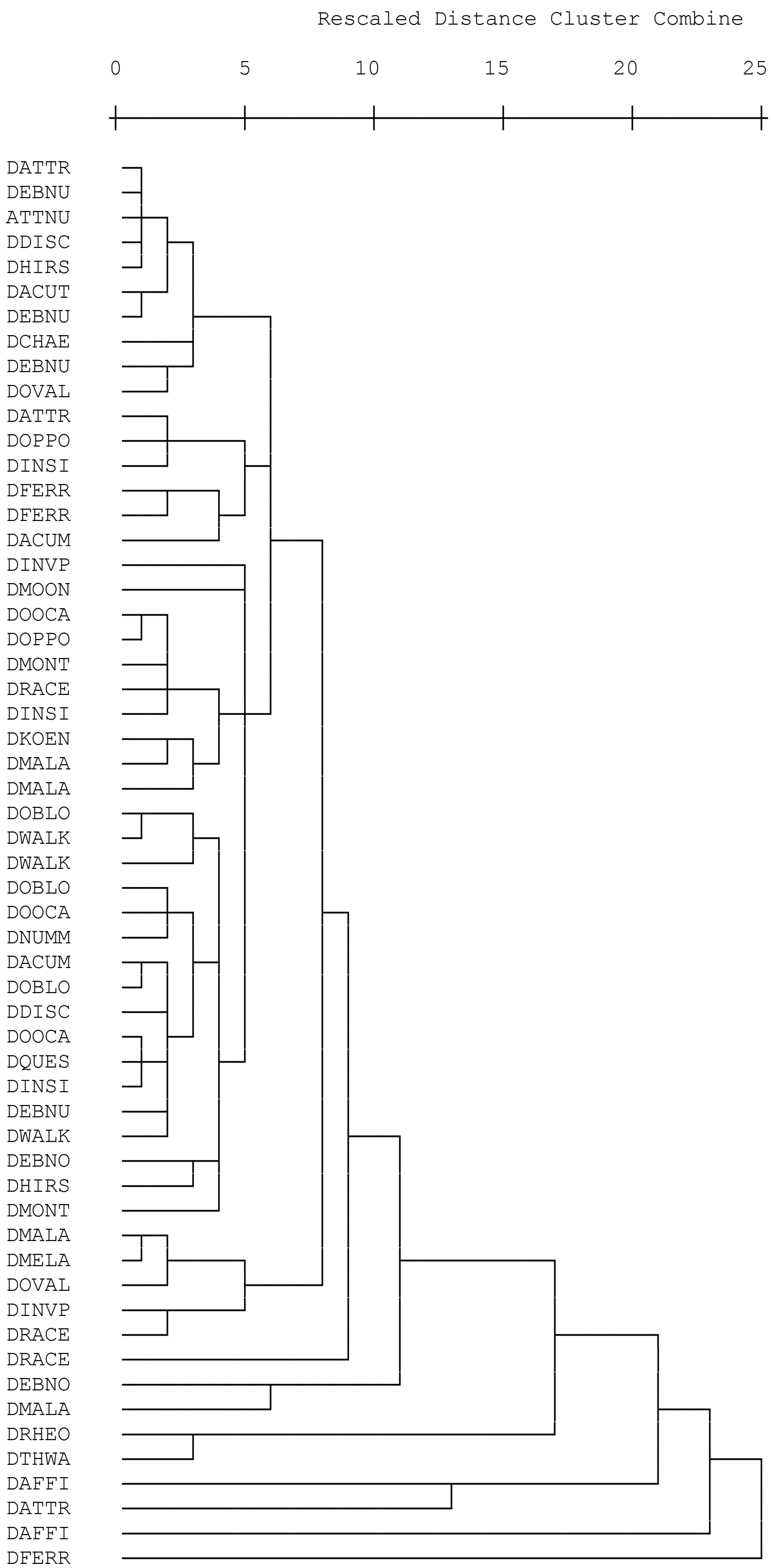


Figure 4. Dendrogram based on 13 wood anatomical characters of 58 *Diospyros* L. specimens.

Table 4. Principal Component Analysis of 13 quantitative wood anatomical characters of the genus *Diospyros* L.

Component	PC1	PC2	PC3	PC4	PC5
% variability explained	25.8	16.5	11.3	10.0	7.8
Cumulative%	25.8	42.3	53.6	63.6	71.4
DFPO	**.85444**	.01995	-.27438	.26724	-.01394
NGPA	**.82585**	-.07640	-.22702	.26563	.03874
TVEL	**-.80365**	-.10458	-.03101	.18217	.13401
FDIA	**-.68512**	.22392	-.08122	.21299	-.15597
RHCE	-.08323	**.88622**	.08822	-.06011	.07625
RHMM	-.14091	**.83826**	.21480	.10138	.14959
GSRT	-.36092	**-.50267**	.35952	.11301	.15506
RPMM	.09078	.13689	**.78069**	.12307	-.27920
FLEN	-.16790	.14691	**.69696**	.06438	.14092
NSPA	.30555	.35471	**-.54965**	.28028	-.33151
VDIA	-.05679	.05974	-.10736	**-.84012**	-.04924
VWTH	.41839	-.32269	-.02985	-.43411	.33830
RWMM	.03499	.17232	-.00043	.03343	**.88867**

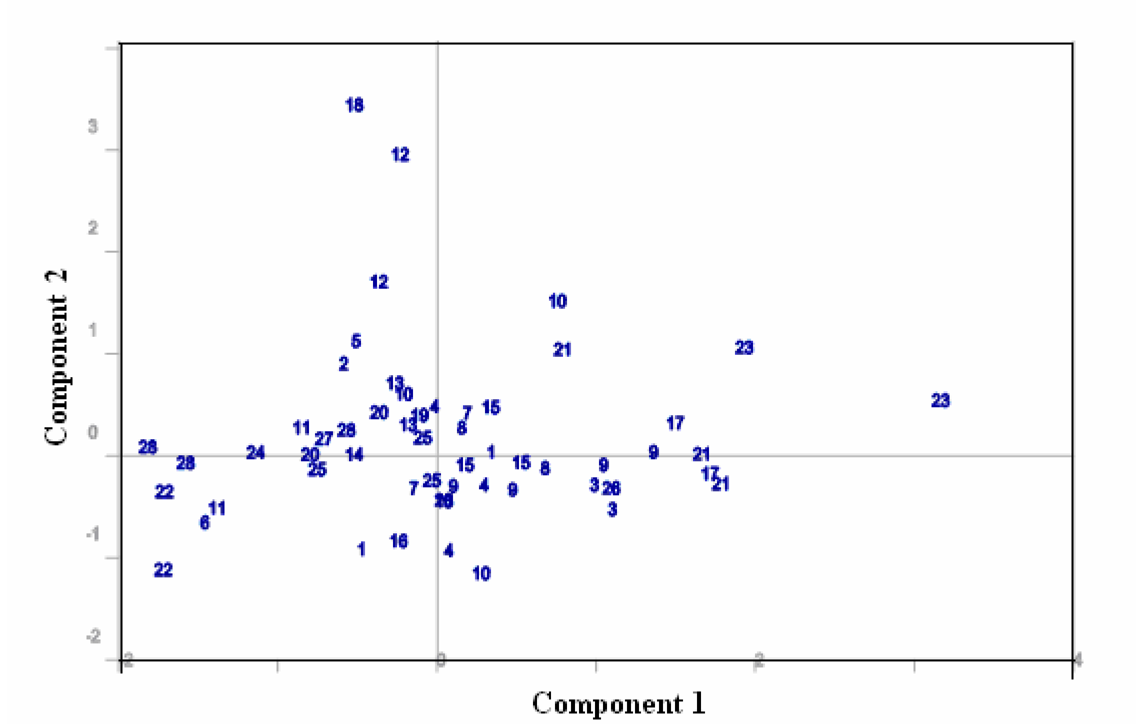


Figure 5. PCA Scatter Diagram produced by plotting the first PC against the second PC for wood anatomical characters.

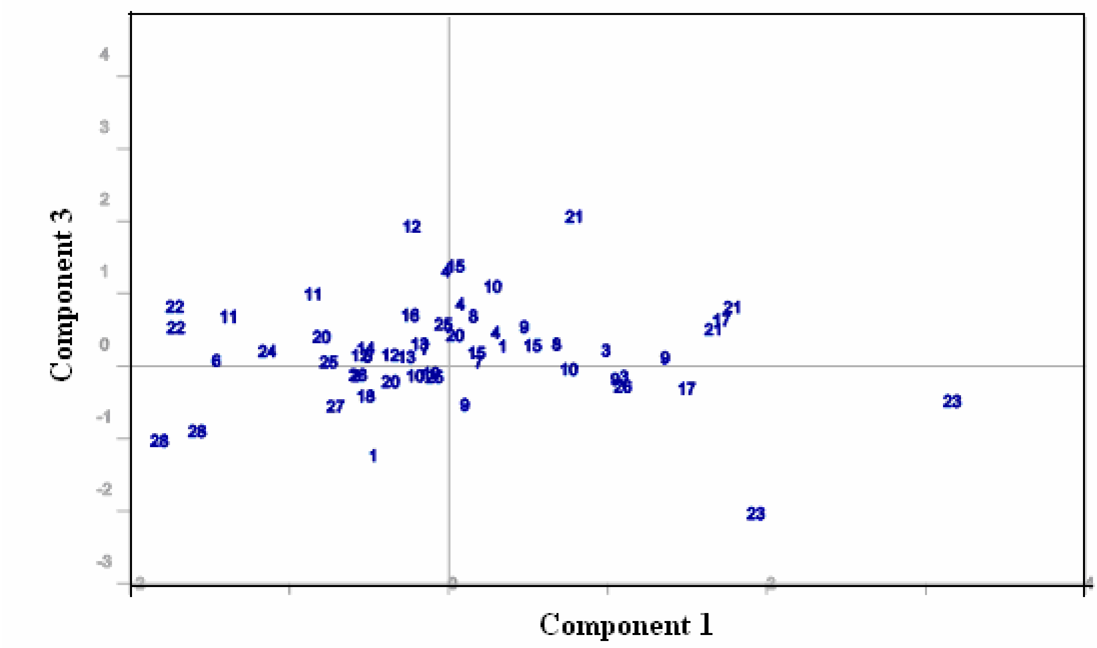


Figure 6. PCA Scatter diagram produced by plotting the first PC against the third PC for wood anatomical characters.

D. ovalifolia which is widely distributed in the dry zone falls into a separate cluster (23 in Fig. 5 and Fig. 6) which is isolated from the rest of species. PCA of wood anatomical characters clearly indicates that *D. ovalifolia* is easily distinguished from the rest of the species of the genus. Further analysis shows that the rest of the species form a large cluster and reflects their wood anatomical similarities.

The results of the Discriminant Analysis (DA) of quantitative wood anatomical data (Table 5) showed that, 8 out of 13 characters are significant at $P < 0.05$, indicating that these characters are more important in separating the species. Based on the outcome of the Discriminant Analysis, three discriminant scores were calculated for each specimen. Using the discriminant scores derived, two scatter plots were produced *viz.* discriminant function one with discriminant function two and discriminant function one with discriminant function three respectively (Fig. 7 and Fig. 8). The specimens of *D. atrata* and *D. malabarica* are grouped together showing their wood anatomical similarity (4 and15 in Fig. 5). *D. atrata* is an endemic and restricted to the intermediate and the wet zone of the island. According to Kostermans (1981), *D. malabarica* is widely distributed in the dry and the intermediate parts of Sri Lanka and also in India, Thailand, Indo-China and Western Malaysia. Based on the above facts, it could be tentatively concluded that *D. malabarica* would be the basic stock from which the other *Diospyros* species arose through the endemic *D. atrata*.

Separate grouping pattern of *D. oocarpa* and *D. montana*, isolated positioning of *D. ovalifolia* and the same grouping pattern of *D. walkeri* were also reflected in both PCA and DA. The rest of the species falls into a single large group (Fig. 7 and Fig. 8) showing the ambiguity of their interrelationships.

Results of the Discriminant Analysis of Qualitative data showed that out of 13 characters 7 were significant at $P < 0.05$ in the separation of the species within the genus (Table 6). The results indicate that intervascular pitting does not significantly vary within the genus and could be neglected in the analysis. Scatter plots derived from the Discriminant Analysis clearly showed that there is no particular grouping pattern in the data concerned.

The results of the analysis with wood anatomical data and ecological origin assigned to the specimens showed that pore distribution frequency, fiber to vessel length ratio, number of groups per area, vessel element length and vessel wall thickness significantly ($P < 0.05$) vary with the ecological condition of the habitat (Table 7). The scatter plots derived from this analysis reflected only the dependence of wood anatomical characters on ecological conditions of the habitat. The intermediate zone specimens showed a tendency of merging with the dry zone specimens rather than the wet zone specimens. Based on the above findings it could be concluded that the wood anatomical variation within the genus is of less importance in delimitation of the taxa. Further, these results are in compliance with findings which have already been discussed under individual characters.

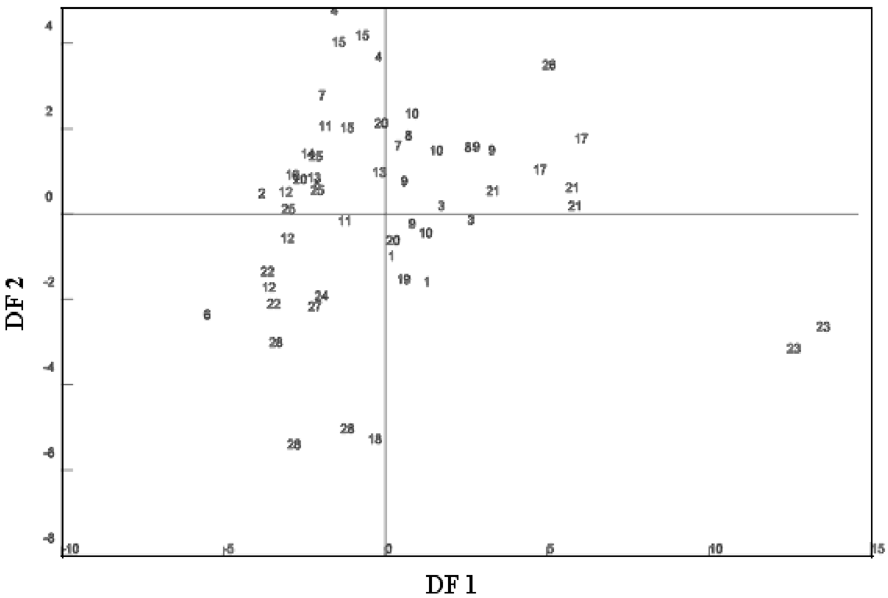


Figure 7. Scatter diagram produced by plotting Discriminant Function one against Discriminant Function 2 for quantitative wood anatomical characters

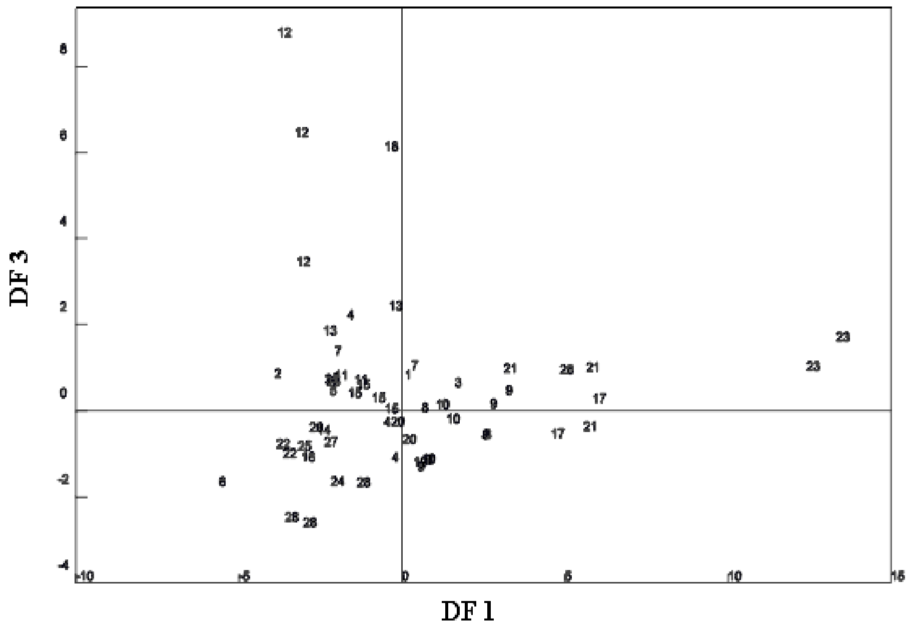


Figure 8. Scatter diagram produced by plotting Discriminant Function one against Discriminant Function three or quantitative wood anatomical characters.

Table 5. Discriminant Analysis of 13 quantitative wood anatomical characters of the genus *Diospyros* L. Shows significance of quantitative wood anatomical characters used in Discriminant analysis (Wilks' Lambda (U-statistic) and univariate F-ratio with 27 and 29 degrees of freedom).

Variable	Wilks' Lambda	F	Significance
DFPO	.09906	9.7682	.0000
FDIA	.21212	3.9894	.0002
FLEN	.49479	1.0967	.4026
NGPA	.16245	5.5377	.0000
NSPA	.35452	1.9556	.0398
RHCE	.19779	4.3563	.0001
RHMM	.31332	2.3540	.0130
RPMM	.73652	0.3842	.9927
RWMM	.67344	0.5208	.9539
TVEL	.20776	4.0958	.0002
VDIA	.40418	1.5834	.1137
VWTH	.31791	2.3045	.0149
GSRT	.38641	1.7056	.0808

Table 6. Discriminant Analysis of 13 qualitative wood anatomical characters of the genus *Diospyros* L.. Shows significance of qualitative wood anatomical characters used in Discriminant analysis (Wilks' Lambda (U-statistic) and univariate F-ratio with 27 and 29 degrees of freedom).

Variable	**Wilks' Lambda**	**F**	**Significance**
CRYS	.29530	2.5631	.0073
FIBT	.41912	1.4886	.1477
GRRI	.25743	3.0982	.0018
PABA	.00333	321.0351	.0000
PADI	.07250	13.7418	.0000
PEPL	.36352	1.8806	.0492
PITS	is a constant.		
PIVE	.67857	0.5088	.9593
RAGE	.50893	1.0364	.4609
RASE	.60455	0.7026	.8202
TRAC	.22814	3.6339	.0005
TYLO	.24449	3.3191	.0010
VEDI	.24359	3.3353	.0010

Oever *et al*., (1981) and Carlquist and Hoekman (1985) working with Symplocaceae and Staphylaceae respectively showed significant correlations among wood anatomical characters, such as vessel wall thickness to vessel diameter, vessel diameter to distribution frequency, vessel element length to fiber length and tracheary element length and vessel element length to ray height.

Table 7. Discriminant Analysis of wood anatomical characters against ecological zones of the genus *Diospyros* L. Shows significance quantitative wood anatomical data in relation to ecological origin of specimens (Wilks' Lambda (U-statistic) and univariate F-ratio with 2 and 54 degrees of freedom).

Variable	Wilks' Lambda	F	Significance
DFPO	.53284	23.6723	.0000
FDIA	.86836	4.0931	.0221
FLEN	.96153	1.0802	.3468
FVRAT	.77686	7.7554	.0011
NGPA	.58267	19.3388	.0000
NSPA	.91300	2.5727	.0857
RHCE	.96929	.8555	.4307
RHMM	.92733	2.1159	.1304
RPMM	.90015	2.9949	.0584
RWCE	.90975	2.6786	.0778
RWMM	.97369	.7296	.4868
TVEL	.67061	13.2620	.0000
VDIA	.93179	1.9764	.1485
VWTH	.76149	8.4569	.0006

Somaratne and Heart (2001) showed a higher significant correlation at P < 0.001, among vessel element length, fiber length and tracheary element lengths and significant correlation at P < 0.01 between height of ray and vessel element lengths; vessel diameter and fiber diameter in *Calophyllum L*. species in Sri Lanka.

The correlation coefficients between fiber diameter and vessel element length and fiber diameter and number of vessel groups per area were significantly correlated at P < 0.05 in the present study. A correlation coefficient at P < 0.05 level was observed for fiber diameter and vessel wall thickness. These findings do not support the findings of the above mentioned work for the genus and further studies are needed to make conclusions. Evidence is available to a certain extent that there is a relationship between wood anatomical variation and latitudes and latitudes (Metcalf and Chalk 1989; Graff and Baas 1974; Oever *et al*., 1981).

genus *Diospyros* L. in relation to altitude isnegligible. This may be due to the narrow altitudinal distribution of the species studied as all the specimens collected occurred in the area below 700 m in elevation. Graff and Baas (1974) pointed out that the elevation differences of the specimens should be at least more than 2000 m to obtain a significant dependency of wood anatomical characters on altitude. Significant correlation coefficients were obtained for mean annual rainfall and vessel element length (P < 0.05) and mean annual rainfall and vessel distribution frequency (P < 0.05). A strong correlation coefficient has also been observed among wood anatomical characters with mesomorphy and conductance.

The results of the study showed a decrease in vessel element length and vessel diameter with decrease of water availability (Fig. 9). These are in agreement with findings of Carlquist and De Buhr (1977). Figure 10 shows the relationships among mesomorphy indices, conductance and mean annual rainfall.

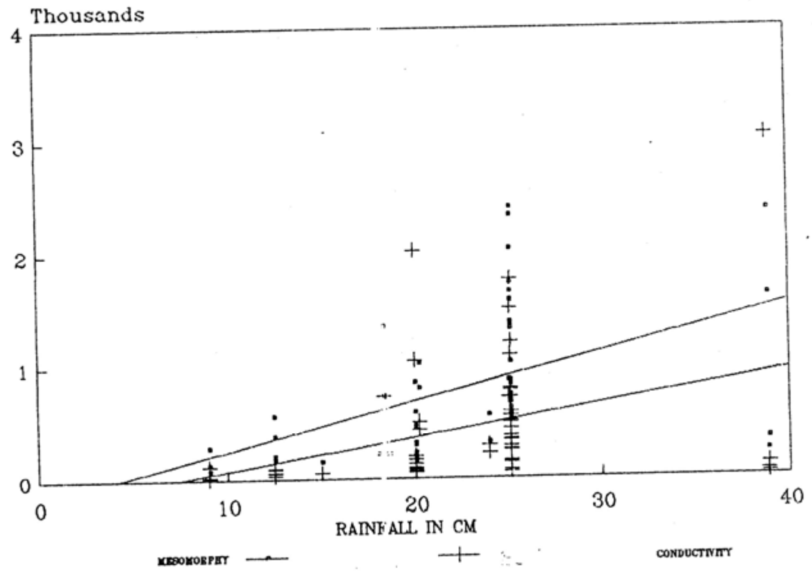


Figure 9. The relationship among rainfall, vessel element length and vessel diameter.

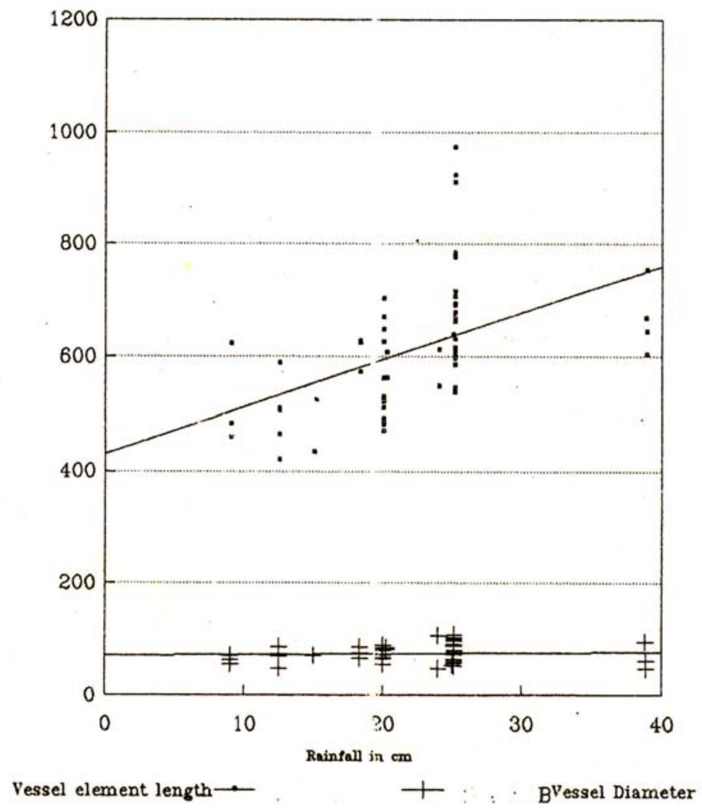


Figure 10. The relationship between rainfall, mesomorphy and conductivity.

It is evident that there is a clear relationship between mesomorphy index and also with conductance i.e. an increase in mean annual rainfall causes an increased mesomorphy index and conductance. As these findings agree with the idea of Carlquist and De Buhr (1977), both mesomorphy indices and conductance values could be used to ascertain the ecological origin of a species of the genus under consideration.

The relationships among agro-ecological zones versus mesomorphy and conductance values also show a linear pattern. Carlquist (1984) pointed out that vessel grouping and presence of vasicentric tracheids play an important role in water conductive efficiency and believed that in case of air embolism of vessel elements, the neighboring vasicentric tracheids which will resist the spreading of air bubbles along the lumen could be of importance in maintaining the function of the disabled vessel element. Present study reveals that, vessel grouping is greater in dry zone specimens rather than wet zone species. Further, appearance of tracheids is sporadic and it could be believed that these structures are of certain value in compensating for the disabled vessel elements. Lack of tracheids may be considered as a contributive factor which increases vessel grouping of the dry zone species of the genus. Further, it is observed that in the dry zone species, vessel groups consist of vessels with different diameters. Functionally this arrangement of vessels will be a mechanism to maintain the continuous water flow in case of air embolism of larger vessels which are susceptible to such conditions. This structural organization of the vessel arrangement could be correlated with the drought resistance ability of some species of the *Diospyros* taxa of Sri Lanka. Further studies on these lines are required for better understanding of the ecological adaptive ability of wood anatomical characters.

As a whole, it should be pointed out that the wood anatomical characters of the taxa of the genus *Diospyros* are highly correlated with the environmental conditions of the habitat, especially with water availability. Characteristic features of vessel elements and fiber lengths cannot be used as an indication of evolutionary advancement of the Sri Lankan endemics of the genus. Such evolutionary trends cannot be traced among the endemic taxa in order to establish evolutionary relationships between the endemic and non-endemic Sri Lankan *Diospyros* species. Further studies on comparative anatomical studies of other vegetative and reproductive parts may be of importance in delimitation of *Diospyros* in Sri Lanka.

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